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THE ENTERON AND INTEGUMENT OF CRYPTOBRANCHUS ALLEGHENIENSIS

By ALBERT M. REESE

WITH TWO PLATES

It was the original intention of the writer to make a detailed study of the histology of the Giant Salamander, but the unexpected appearance of much more interesting and important work has necessitated a change of plans. It has seemed best, instead of indefinitely postponing the present research, to make a less detailed study of the enteron and integument, the two regions upon which work had already been begun.

The material was collected from the tributaries of the Allegheny river, in western Pennsylvania. The chief fixing fluids used were: corrosive sublimate, corrosive-acetic mixture, Perenyi's fluid, and picro-sulphuric acid. The tissues were mostly cut in paraffin, and stained with borax carmine and Lyon's blue.

THE ENTERON

ORAL CAVITY

The lining of the oral cavity presents no particularly striking or interesting features, and a brief description of this region will suffice. The lining mucous membrane consists of a stratified epithelium of about four or five layers, the nuclei of which are large and very irregular in outline. The rest of the wall consists of connective tissue which is very dense next to the epithelium while on the side away from it it is of a much looser character and contains numerous large nuclei.

TONGUE

The tongue covers the greater part of the floor of the mouth and is supported by the well developed hyoid apparatus, from which, in an animal of average size, it projects freely forwards for about one centimeter. It is covered by a slightly wrinkled layer of mucous membrane. Since it is free for so short a distance from the hyoid apparatus, it has very little power of motion apart from what is given by that apparatus, and its musculature is, in consequence, not strongly developed.

A section through the mucous membrane of the tongue is shown in Pl. X, fig. 1, together with several of the small bundles of muscle fibres (*m*). The epithelium is, as might be expected, stratified, and is so deeply folded that it seems, when seen in section, to form a great number of irregular tubular glands (*g*). All of the cells of the epithelium seem capable of secreting mucous, with which they become so swollen and distended that they resemble somewhat adipose tissue, except that they retain their angular outlines. The cells of the gland-like folds, *g*, are so distended with secretion that they form a foam-like reticulum in the meshes of which a few scattered nuclei are seen. The superficial cells may show at places a fairly typical stratified structure, as at the end of the reference line *s*; at such places there is some indication of a thin cuticular border, though it is not shown in the figure.

No trace of the sense organs described by Kingsbury (94) in the tongue of *Necturus* were found, though they may have been present in other regions than those represented in the sections studied. The mucous membrane is supported by a thick corium (*c*) of comparatively dense connective tissue, composed of fine fibres with a few scattered nuclei. Through this corium are scattered blood vessels, and in its lower part are collected a few rather small bundles of muscle fibres (*m*), all of which seem to extend in the same direction. The figure shows the relatively slight development of the muscular tissue.

OESOPHAGUS

The oesophagus, which is comparatively short, is separated from the pharynx by a fairly well marked constriction, while from the stomach it is not so sharply separated. Its mucous membrane, especially in the region adjacent to the stomach, is thrown into numerous, deep, longitudinal folds. These folds, shown in Pl. X, fig. 2, are frequently spread out at the bottom into secondary folds, giving the appearance of long glands; the oesophageal glands described by Kingsbury (94) in *Necturus* are not present in *Cryptobranchus.*

A transverse section of the oesophagus is shown in Pl. X, fig. 2. Three chief layers may be distinguished: An outer longitudinal muscle layer (*e*), which might be called the fibro-muscular, as it is made up of rather scattered bundles of muscle fibres separated by trabeculae of connective tissue fibres; in fact this layer more resembles a very thick serosa than a layer of longitudinal muscle fibres. The second layer, lying, of course, just inside of the longitudinal muscles, is the layer of circularly arranged muscle fibres (Pl. X, fig. 2, *c*); this layer is sharply defined, and is composed of closely packed muscle fibres of the involuntary type. The third and innermost layer is the mucosa (*m*), composed of a lining epithelium supported by a comparatively thick mass of connective tissue.

The mucosa is the only layer that need be described in any further detail. The lining epithelium of the mucosa is of the ciliated stratified variety, instead of the simple ciliated columnar type that is described in *Necturus* by Kingsbury. It is thrown into deep folds (Pl. X, fig. 2) to conform to the longitudinal folds of the mucosa that have already been mentioned. Three kinds of cells may be distinguished, ciliated columnar, goblet, and irregular basal cells (Pl. X, fig. 3). The columnar cells (Pl. X, fig. 3, *c*) are irregularly pyramidal in shape, the narrow base of the pyramid being the exposed side which is covered with rather short, fine cilia. The nucleus is large, coarsely granular, and lies in about the middle of the cell, which it bulges out at that place. The pointed end of the cell projects down among the lower cells, so that it is difficult to determine its outline. The cytoplasm is finely granular. The goblet cells (Pl. X, fig. 3, *b*) vary in number in different regions, being sometimes almost wanting, and again, being quite as numerous as the ciliated columnar cells just described. They vary in shape with the amount of secretion they contain; they have the appearance of being columnar cells which have become distended, beginning at the free end, with a clear secretion. The cell figured is a typical goblet cell of this region of the enteron. It shows the free end of the cell enlarged by the contained mass of secretion, while the lower or middle part of the cell is bulged out by the nucleus, as in the ordinary columnar cell. Between the nucleus and the terminal mass of secretion is small mass of protoplasm that still shows a granular structure. The irregular basal cells (Pl. X, fig. 3, *a*) have no definite shape; they are usually nearly filled by their contained nuclei, and are apparently arranged in about two rows.

The tunica propria, or layer of connective tissue that supports the epithelium, consists of a fairly compact mass of fine fibres with numerous nuclei and small blood vessels. The muscularis mucosa, if present, is represented by such scattered fibres that it cannot be determined; there is, therefore, no distinction between the tunica propria and the usual submucosa.

STOMACH

There is no externally visible line of demarkation between the stomach and the oesophagus. When empty the stomach is an elongated organ whose walls, externally, are rather smooth and fibrous, while internally they are thrown into many complicated folds.

The usual layers of the stomach may be made out, and are shown in Pl. X, fig. 4. The fibrous or serous coat can hardly be said to exist as a distinct layer, though the outer or longitudinal muscular layer (*l*) is often made up of almost as much fibrous as muscular tissue, and might be called the fibro-muscular layer: this layer is of about the same thickness throughout the stomach. The circular layer of muscles (*c*) is much more strongly developed than the longitudinal, and increases markedly in thickness in passing from the cardiac to the pyloric end. The muscular coats are, of course, composed of involuntary fibres. The submucous coat (*sm*), is of the usual character, and is well developed: it becomes somewhat thinner towards the pyloric end of the stomach. The muscularis mucosa (*mm*) is fairly well developed: it shows an indistinct division into an outer longitudinal and an inner circular layer (this is not indicated in the figure).

It is in the structure of the mucous membrane that the chief differences between the two ends of the stomach are seen. The cardiac mucosa will first be described. It consists of a single layer of columnar epithelium (Pl. X, fig. 4, *e*), overlying a fibrous tunica propria (*m*) and dipping down into the cardiac glands (*g*); the muscularis mucosa has already been mentioned. The epithelium (Pl. X, fig. 5, *e*), on the free surface, consists of tall, columnar cells whose outer ends are more or less clear, while the inner ends are finely granular. The nuclei are large, and lie in the lower half of the cells, in some cases, in other cases in the middle of the cells. The cardiac glands are of the usual compound tubular character; they are moderately long, and are not nearly so closely aggregated as in the higher animals (Pl. X, fig. 4). Each gland (Pl. X, fig. 5) may be divided into three regions; the neck or duct (*n*), the mucous region (*s*), and the fundus (*f*). The duct or neck is comparatively wide and may form half the entire length of the gland; it is lined with the same cells as those that have been described as covering the free surface of the mucous membrane. Two, or possibly three, ducts may unite to form one opening to the surface. Below the neck the gland is considerably enlarged by a collection of clear, mucous cells, shown rather diagrammatically in the figure at *s*; this is the mucous region. These mucous regions which are more strikingly marked off from the rest of the glands than is indicated in the figure form a very characteristic feature of the cardiac end of the stomach. The mucous cells are large and irregular in shape (not well shown in the figure); each cell contains, near its base, a nucleus which is smaller and more rounded than those of the neck region. The swollen, globular character of the mucous region is much more marked in the form under discussion than in *Necturus* as described by Kingsbury. The deeper or fundic region (Pl. X, fig. 5, *f*, *f'*) is elongated, convoluted, and frequently branched; it is narrower than the rest of the gland, and, owing to its convolutions, is seldom cut through its entire length by any single section. The cells of this region are irregularly cuboidal in shape, and contain nuclei of the same general character as those of the mucous region. The cells are filled with granules which are somewhat coarser than those of the neck region, but no distinction into a clear outer and a granular inner zone is to be made out in the preparations at hand.

The mucous membrane of the pyloric end of the stomach (Pl. X, fig. 6) is much thinner than that of the cardiac region, and differs from it markedly in structure; there is, however, no sharp line of demarkation between the two regions, the cardiac glands changing gradually to the form characteristic of the pyloric region. The entire pyloric gland practically corresponds to the neck region of the cardiac gland. Near its bottom it narrows suddenly, and sometimes branches; these branched portions are always short. The epithelium is of the tall columnar variety; the nuclei are located in the bases of the cells, where the small amount of granular protoplasm is collected. The outer half of the cells (*e*) is clear and mucigenous; the free ends being rounded and often constricted to form a sort of knob, as shown at *e*. This clear zone is much deeper and more strongly marked in this region than in the cardiac portion of the stomach, though it is not very distinct in the narrow, branched portion of the glands (*f*). The fibrous tunica propria that supports the epithelium and glands (*m*) is of the same character as in the cardiac region, but is, of course, thinner.

INTESTINE

While the stomach, as has been said, is not sharply marked off from the oesophagus, it is sharply differentiated, even externally, from the intestine by a well marked constriction. The intestine is quite narrow, though its diameter varies considerably, and, in an animal of average size, is about thirty-five centimeters in length. Externally the intestine has the usual smooth appearance, while internally it is thrown into numerous longitudinal folds (Pl. XI, fig. 7). The size of the lumen varies greatly, being sometimes reduced to a very narrow passage (Pl. XI, fig. 7), while again it may be surprisingly wide.

Pl. XI, fig. 7 is a camera drawing of a transverse section to show the relative thickness of the various layers and the irregular outline of the lumen. The outermost layer (Pl. XI, fig. 8, *s*) is a very thin fibrous coat, so closely adherent to the outer muscular layer that it is easily overlooked. The longitudinal and circular muscular layers (Pl. XI, figs. 7 and 8, *l* and *c*) are of about equal thickness, the former being composed of scattered muscular fibres among which are numerous connective tissue fibres and blood vessels, and the latter of a compact mass of circularly arranged muscle fibres. The submucosa has the usual appearance of that layer; it is thrown into the deep longitudinal folds that have already been mentioned (Pl. XI, figs. 7 and 8). The epithelium is of the simple columnar type (Pl. XI, figs. 8 and 9), and follows, of course, all the foldings of the fibrous layer against which it lies. A top-plate or striated border (*t*) is very distinct. Two kinds of cells may be recognized; the typical columnar cells, and the goblet cells. The former (Pl XI, fig. 8, *e*, and fig. 9, *a* and *b*) vary considerably in width and shape according to their location; on the sides of the folds they are quite regularly columnar, while those at the top of the folds are narrow at the inner end and wider at the outer, and those at the bottom of the folds are compressed at the free end and wide at the inner end. Each cell is finely granular, and contains a large oval nucleus which lies about in the middle of the regular cells, and towards the broader end of the pointed cells. The goblet cells (Pl. XI, fig. 8, *g*, and fig. 9, *c* and *d*) vary considerably in number and size; the nucleus lies near the basal end, though its position varies in different cells. All stages may be seen, from the columnar cell that is just beginning to become clear and swollen at its outer end, to the fully formed, typical goblet cell.

The glands described by Kingsbury in *Necturus* seem not to be present. They may be represented by certain rather indefinite groups of cells that are occasionally found at the lower angles of the folds (Pl. XI, fig. 8, *n*) ; no indication of a lumen is to be seen in any of these groups of cells, so that it seems more likely that they are, as has been suggested by Bizzozro and Nicolas for other forms, simply groups of young cells from which new epithelial cells are derived.

RECTUM

The intestine, after a slight constriction, merges suddenly into the cloaca or rectum, which is about eight centimeters long in an individual of average length. It is of considerably larger diameter than the intestine, and is sometimes of about equal diameter throughout, sometimes narrower towards the posterior end.

Disregarding the marked folds of the intestine which are not present in the rectum, the walls of the latter region are somewhat thicker than those of the former. The longitudinal folds being absent, as has been said, the lumen of the rectum is much wider than that of the intestine. The serous, muscular, and submucosal layers are about the same as in the intestine, and need not be further described (Pl. XI, fig. 10). The mucosa, which is comparatively smooth because of the evenness of the submucosa, is a stratified epithelium. The superficial cells are of two kinds; irregular, tall columnar cells, and goblet cells (Pl. XI, fig. 11). A marked striated border is present as in the intestine (Pl. XI, fig. 10). The nuclei of the columnar as well as of the goblet cells are oval in shape and situated near the base of the cells. Beneath the superficial layer of columnar and goblet cells are two or three layers of short, irregular cells (Pl. XI, fig. 10, *i*) whose outlines are difficult to determine: each of these cells contains a large round nucleus.

THE INTEGUMENT

The surface appearance of the skin is one of the most characteristic features of the Giant Salamander. The two lateral folds, extending from the front legs to a point some distance back of the posterior limbs, are very striking, and add to the animal's unprepossessing appearance. The general color is a greenish-brown, with dark, irregularly scattered blotches. The color varies in the same individual, being sometimes nearly black, and sometimes of a decided reddish tinge; this change in color takes place in both sexes.

The skin, like that of most of the amphibia, is smooth and slimy, although the slime is not so abundant as in some other forms. The animals, when kept in captivity, shed from the entire body a thin, transparent cuticle, which may be preserved in formalin and used as an excellent demonstration of pavement epithelium, for classes in histology (Pl. XI, fig. 12).

Scattered over practically the entire body, but especially over the head, are numerous small, light-colored papillae, the neuromasts or organs of the lateral line system; their arrangement has been described by Malbranch (76) and Kingsbury (95). Each papilla is about the size of a small pin-head, and is either rounded or oval in shape (Pl. XI, fig. 13, *n*).

A small portion of the integument from the top of the head is represented in Pl. XI, fig. 13. It was cleaned of the underlying connective tissue, dehydrated, cleared, and drawn under a magnification of forty diameters. It shows, in the centre, an oblong papilla (*n*), with a dozen or more glands (*g*) grouped about it. The neuromast shows a slight transverse furrow, but no duct or opening. Nearly all of the glands, on the other hand, show a distinct, and generally elongated, opening (*d*). Scattered among the glands and neuromasts are numerous, black, pigment spots (*p*), which show a tendency to arrange themselves around the glands. There are also numerous brown, finely granular spots among the more striking black spots. It may be a variation in the relative numbers of these two kinds of spots that causes the change in color that has been mentioned. In a portion of the skin viewed, as in the figure, by transmitted light, the glands stand out very markedly as clear circles in a darker background; and while they are not evenly distributed, they are usually very close together, so that they are present in enormous numbers.

A section of the integument, passing through a single neuromast and two glands, is shown in Pl. XI, fig. 14. Three regions may be distinguished; an epidermal layer (*e*), a fibrous layer (*f*), and a muscular layer (*m*). The epidermis varies considerably in thickness in different regions; it shows practically no differentiation into layers, except that the cells on the free surface, next to the cuticle, are slightly flattened. In some regions the cells are irregularly cuboidal, in other regions they are somewhat elongated in a direction perpendicular to the surface. The cuticle (*c*) scarcely shows in sections, except where it is slightly separated from the underlying cells. The fibrous or connective tissue layer is made up of a loose mass of fibres, through which are scattered the large, black pigment cells (*p*) that have already been mentioned. Into this layer project the glands and neuromasts from the epithelial layer. The muscular layer varies somewhat in thickness in different regions. and is made up of a rather definite mass of intertwining fibres.

The glands are either of two distinct kinds, or they vary in appearance in the different stages of their activity. At *g* is shown a gland that is cut through the centre, showing its opening to the surface (*d*). This gland, which happens to be empty of secretion, shows the layer of irregular cells (*s*) that form its outline, and the funnel-shaped opening through the epidermis. The cells of the glandular wall seem to project into the mouth of this funnel, and are, at this place, two or three layers in depth (*t*) ; Schneider (02) calls these cells, that really form the beginning of the duct, the " intercalary cells." The cuticle passes down into the duct, between the intercalary cells and the epidermis. Surrounding the epithelium of the gland is a fairly distinct basement membrane, but the muscular layer that is sometimes described cannot be made out. The nuclei of the glandular cells are small and irregularly oval in shape. A second gland is shown at *g'*. This gland is cut through one side, so that it seems smaller than the other, and does not show its duct. The secretion with which this gland is filled is granular in appearance, and takes stains readily, so that it always has a decided color. The secretion of the gland first described, on the other hand, is very slightly affected by stains, and is not so markedly granular in appearance. The nuclei of the second kind of gland are less numerous than those of the first, and are considerably larger and more rounded in shape.

The neuromast that is represented in Fig. 14 is cut in a plane at right angles to its long axis. It does not show as marked an elevation above the general surface of the skin as might be expected. It will be noticed that the epidermis dips down, and, becoming reduced to a single layer of cells, forms the outer wall of the neuromast. A comparatively wide opening connects the cavity of the organ with the exterior. The structure of the neuromast is essentially the same as that described by Schneider (02) and Kingsbury (95) for other Urodela. The main body of the organ is made up of elongated supporting cells (*r*), whose nuclei form a more or less regular row at the outer ends. The elongated cytoplasmic portions of these cells do not stain readily, so that it is difficult to determine accurately the cell boundaries. At the bottom of the cavity of the neuromast, among the inner ends of the central supporting cells, is a small group of cells (*o*) which doubtless correspond to the "sensory cells" of other workers. They are small, conical cells, with deeply-staining nuclei. Their pointed ends often project slightly into the cavity of the neuromast. The nervous supply of the organ cannot, with the material at hand, be definitely determined, but a rather indefinite mass of fibres and cells (*n*) extending from the bottom of the neuromast may indicate the position of the entering nerve.

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EXPLANATION OF PLATES

Plate X

Fig. 1. Vertical section through the dorsal surface of the tongue: *c*, sub-epithelial connective tissue, containing many blood vessels; *g*, glandular foldings of the epithelium; *m*, bundles of muscle fibres; *s*, ordinary columnar epithelium; *s′*, irregular, swollen epithelial cells at the opening of one of the glands.

Fig. 2. Transverse section through the well of the oesophagus: *c*, circular muscle fibres; *e*, epithelium; *l*, layer of longitudinal muscle fibres; *m*, layer of sub-epithelial connective tissue.

Fig. 3. Epithelium of the oesophagus: *a*, section through the entire thickness of the epithelium; *b*, a single goblet cell; *c*, a single columnar cell.

Fig. 4. Transverse section through the wall of the cardiac end of the stomach, to show the general arrangement of the different layers: *c*, layer of circular muscle fibres; *e*, epithelium; *g*, cardiac glands; *l*, longitudinal layer of muscle fibres—the thin outer border of this layer represents the fibrous or serous layer; *m*, fibrous tunica propria; *mm*, muscularis mucosa; *sm*, submucosa.

Fig. 5. Vertical section through the mucous membrane of the cardiac region of the stomach, showing the structure of the cardiac glands: *e*, superficial epithelium; *f*, fundus of a gland, cut longitudinally; *f′*, transverse section through the fundus of a gland; *m*, tunica propria; *n*, duct of the gland; *s*, swollen mucous cells.

Fig. 6. Vertical section through two glands of the pyloric region of the stomach: *e*, epithelium, composed of a single layer of columnar cells with a clear outer and a granular inner zone, the latter containing the nucleus, the outer zone being, in many cells, constricted to form a sort of knob-like end; *f*, narrow fundus of gland, cut transversely; *m*, fibrous tunica propria; *n*, open neck of gland.

Plate XI

Fig. 7. Transverse section through the entire intestine, to show the relative thickness of the different layers and their general arrangement: *c*, circular muscular layer; *d*, lumen of the intestine; *l*, longitudinal layer of muscle; *m*, fold of the mucous membrane; *s*, mesentery.

Fig. 8. Transverse section through a portion of the intestinal wall, to show the details of structure in two of the longitudinal folds: *a*, blood vessels; *c*, circular muscular layer; *e*, epithelium; *g*, goblet cell; *l*, longitudinal muscle layer; *n*, group of young cells; *s*, serosa; *sm*, submucosa; *t*, top-plate or striated border.

Fig. 9. Isolated cells from the epithelium of the intestine: *a* and *b*, columnar cells; *c* and *d*, goblet cells.

Fig. 10. Transverse section through the wall of the rectum or cloaca: *c*, circular muscle layer; *e*, superficial layer of columnar cells of the mucous membrane; *i*, deeper layers of rounded cells of the epithelium; *l*, longitudinal muscle layer; *s*, serosa; *sm*, submucosa.

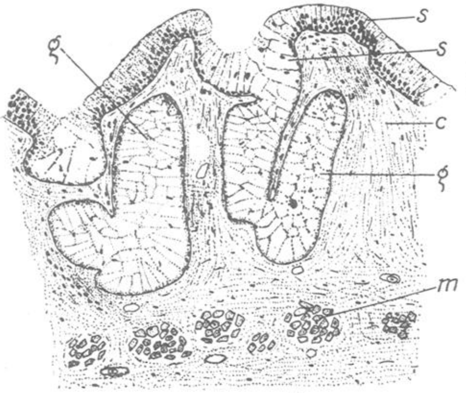
Fig. 11. Isolated cells of the rectum: *a* and *b*, columnar cells; *c*, goblet cell.

Fig. 12. Surface view of cuticle of integument.

Fig. 13. Surface view of the integument as seen under the low power of the microscope; cleared in xylol and viewed as a transparent object: *d*, opening of a gland; *g*, a gland; *n*, an oblong papilla; *p*, pigment spot.

Fig. 14. Vertical section of the integument, passing through a single neuromast and two glands: *c*, cuticle, represented in surface view in Fig. 12; *d*, duct of larger gland; *e*, stratified epithelium; *f*, fibrous supepithelial layer; *g*, a large gland; *g′*, a small gland; *m*, layer of muscle fibres; *n*, nerve (probably) to neuromast; *o*, sensory cells of neuromast; *p*, pigment cells; *r*, supporting cells of neuromast; *s*, cells of the wall of the gland; *t*, "intercalary cells" of gland.

PLATE X



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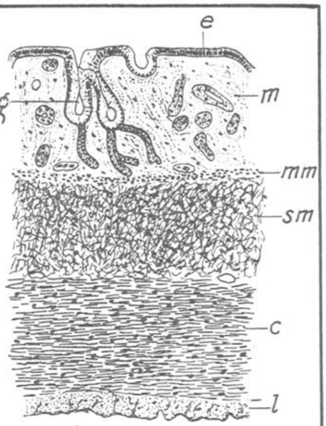

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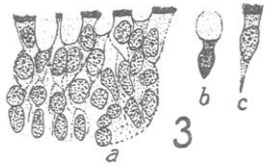

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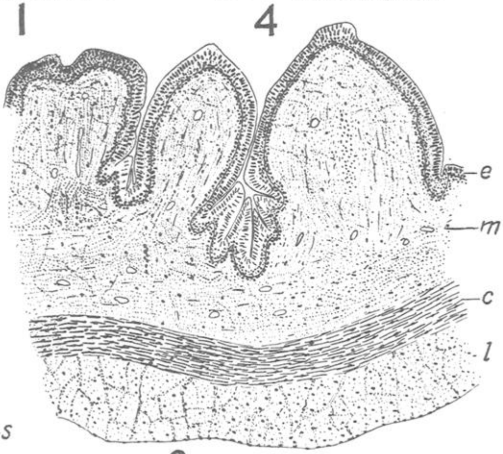

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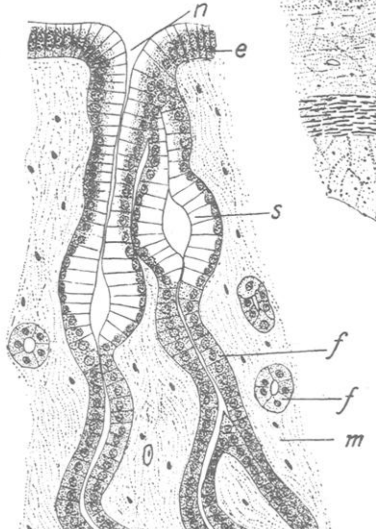

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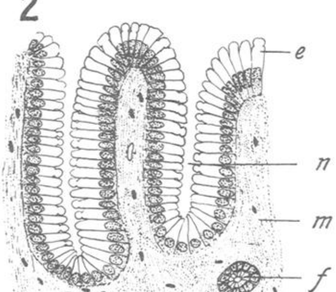

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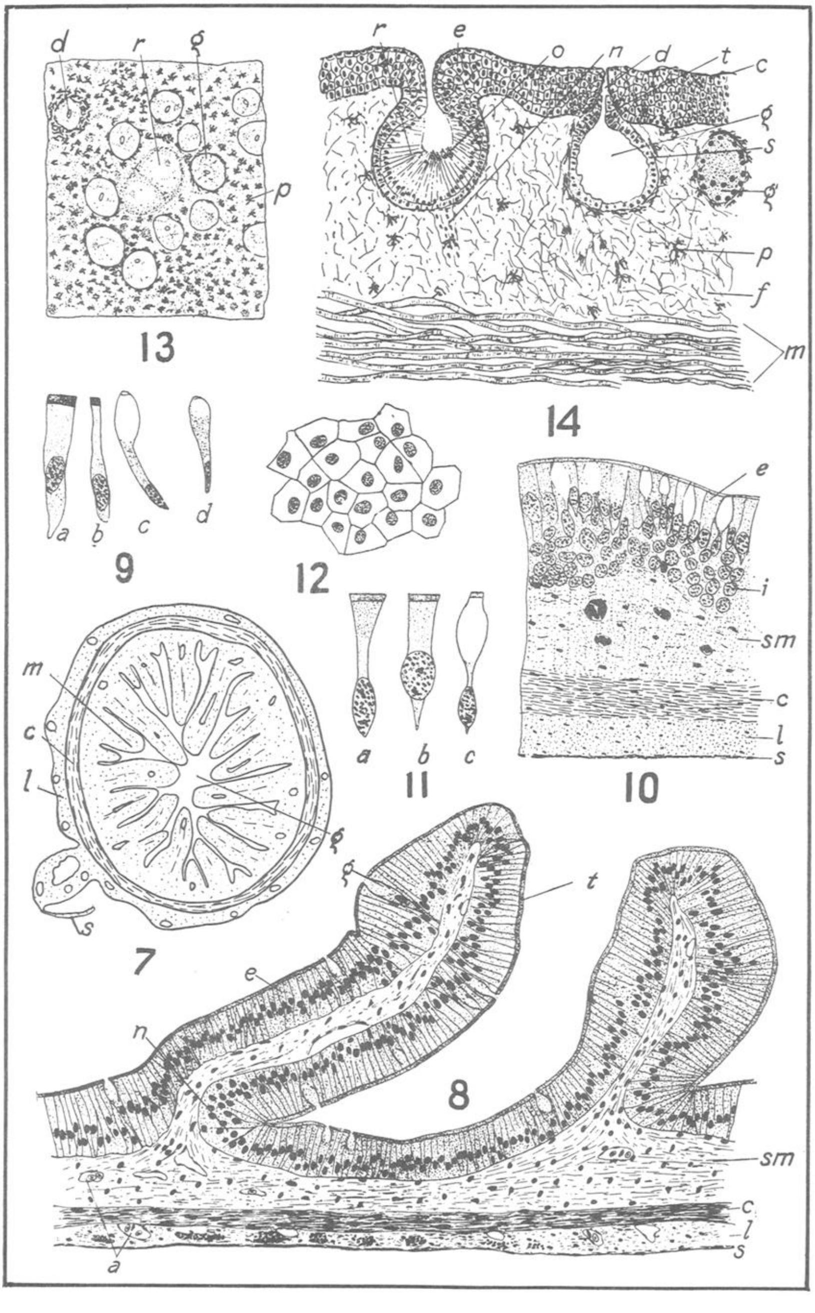
PLATE XI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